

## CORAL REEF SPONGES OF THE SAHUL SHELF — A CASE FOR HABITAT PRESERVATION

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Hooper, J.N.A. 1994 06 30: Coral reef sponges of the sahul shelf — a case for habitat preservation. *Memoirs of the Queensland Museum* 36(1): 93-106. Brisbane, ISSN 0079-8835.

Three adjacent coral reef systems were surveyed (Ashmore-Cartier-Hibernia reefs) on the Sahul Shelf, northwestern edge of the Australian continental plate. 138 species of sponges (Porifera) in 77 genera and 38 families were found. Although sponge species diversity was similar between each of reef system, there was low congruence in species composition despite their close proximity (about 50km apart): Ashmore-Hibernia (13%); Hibernia-Cartier (24%); Cartier-Ashmore (9% similarity). The sponge fauna was divisible into four faunistic groups. 1. Widely distributed Indo-west Pacific species, known from Burma to New Caledonia, including apparently opportunistic species found predominantly on coral substrates. 2. Large populations of autotrophic sponges, characteristic of the shallow water, inner sandy zone and intertidal zones on the reef flat, accounting for most of the coral reef sponge biomass and also found on many Indo-west Pacific coral reefs. Together these two groups comprise only about 16% of species. 3. Coastal and shelf species more-or-less widespread throughout tropical Australasia, comprising about 25% of all species recorded. 4. Species found predominantly in restricted or specialised habitats on the reef comprise the greatest diversity (59%) of sponges in these reef systems, but most of these are poorly documented and known from single or few localities and isolated records in the literature. Differences in species composition between the three reef systems were correlated with both major and minor differences in the geomorphology of particular reef systems. These findings suggest that the concept of a 'ubiquitous coral reef sponge fauna' is too simplistic. Different reefs contain different faunas, largely dependent on the presence or absence of particular habitats. These data, using sponges as an example, have implications for the special management of biodiversity in coral reef systems by habitat conservation in preference to preservation of particular taxa in the tropical marine benthos. Evidence presented here questions the validity of preserving only a single reef as being 'representative' of a system of reefs. □ *Porifera. Sahul Shelf, Ashmore Reef, Cartier Island, Hibernia Reef, faunal survey, sponge biodiversity, habitat conservation.*

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As for many other groups of marine invertebrates (Briggs, 1987), northern Australian - southern Indonesian marine habitats may contain the highest diversity of sponge species in Recent seas, and the region is often considered to be the centre of dispersal for Indo-Pacific species (Lévi, 1979). In fact, nearly 2000 nominal species of sponges have been described from this region, but it is still considered to be barely known (Hooper & Lévi, 1994). Large collections of sponges have now been made from the more turbid, nutrient rich shallow coastal waters in both northwest Australia (review in Hooper, 1988) and southeast Indonesia (review in van Soest, 1989, 1990), although many of these species records have not yet been published. Similarly, several large collections of sponges from deeper water reefs on the shelf and slope on the western side of the continent exist, but these too remain largely un-

published (Hooper, unpublished data), whereas sponges living on oceanic coral reefs, on the edge of the western continental margin, have neither been collected nor studied previously. By comparison, sponge faunas from coral reefs on the east coast of Australia are comparatively well known (e.g. Burton 1934; Bergquist, 1969; Bergquist et al., 1988; Wilkinson 1987, 1988; Wilkinson & Cheshire, 1989), as they are in several major reef systems in the western Indian Ocean (e.g. Seychelles, Maldives; see summary in Thomas, 1973).

This is the first published report of a sponge fauna from oceanic coral reefs on the northwestern continental margin of Australia. This paper concentrates on the question of sponge species diversity of three prominent reefs, Ashmore, Cartier, and Hibernia Reefs, comparing differences in species composition between each

reef; examining the various factors that potentially contribute to these differences; and contrasting these differences to the reef geomorphology. These data have implications to the conservation and selection of coral reefs as habitat preserves.

Detailed descriptions of habitats, stations surveyed, and methods of collection are given by Russell & Hanley (1992) and Hooper (1992). Three reef systems were studied. Ashmore Reef was visited in March 1981 (RV 'Hai Kung'), July 1986 (MV 'Coral ReefTel') and August 1987 (MV 'Reef Seeker'); Cartier Island and Hibernia Reef were visited in May 1992 (FV 'Rachel'). Sponges were collected along random transects, using SCUBA, to depths of 30m. Underwater photography, using both 35mm-still and 8mm-video formats, were used to supplement manual collections of samples. Species composition, distribution and abundance of sponges were determined from taxonomic studies of samples (using methods described by Hooper, 1991) and comparative analyses of photographic transects. Only two species were unable to be differentiated from photographic records [*Xestospongia testudinaria* (Lamarek) and *X. bergquistia* Fromont], which are lumped together in this study under the former name. The taxonomic scheme (Table 1) follows Hooper et al. (in press).

## RESULTS AND DISCUSSION

### SAHUL SHELF

Ashmore Reef (12°17'S, 123°02'E), Cartier Island (12°32'S, 123°33'E) and Hibernia Reef (11°58'S, 123°22'E) lie near the outer edge of the Australian continental margin in the Timor Sea, about 350km off the Kimberley coast (840km west of Darwin, 640km NNE of Broome), and 115km from the southern Indonesian island of Roti. These reefs are situated on the Sahul Shelf, at the edge of the Australian plate, at a zone of subduction with the southeastern Indonesian plate (see illustration in Michaux, 1991: fig. 2).

The Sahul Shelf consists of a shallow central basin (called the Bonaparte Depression, <140m depth), rising to ridges 20-50m deep on the outer edges and contiguous with the Kimberley coast on its eastern side. On the northern and northwestern edges of the Sahul Shelf the continental margin drops away rapidly to >2000m depth, where the Australian and Indonesian plates meet (Timor trough). All three reefs lie very close to this drop-off, and they are probably influenced to a greater extent by oceanic upwelling from the

trough, rather than terrestrial runoff as is the case for most reefs closer to the continent.

Ashmore, Cartier and Hibernia Reefs are part of a larger system of exposed coral reefs, submerged coral shoals and drowned reefs running along the northwestern margin of the Australian continent. Although only 9 of these reefs are now fully exposed, classed as 'platform reefs' [Rowley Shoals (Imperieuse, Clerke and Mermaid Reefs; 18-17°S), Browse Island (14°S), Scott Reef (14°S), Seringapatam Reef (13.5°S), Cartier Island, Ashmore Reef and Hibernia Reef], it is thought that this whole area once contained many more active coral reefs during times of lower sea levels, comparable to some areas of the Great Barrier Reef (Edgerley, 1974; Van Andel & Veevers, 1967; well illustrated in Butlin, 1979). Despite the absence of an extensive barrier reef on the Sahul Shelf it is nevertheless still classed as a major reef province (Burrett et al., 1991).

### GEOMORPHOLOGY OF THE REEFS

*Ashmore Reef.* It is a large platform reef (often called a 'shelf atoll'), 27km long, 14km wide, with a large circumferential outer reef, broken only on the northern side, a large shallow, very heavily silted central lagoon, and several sand cays (Fig. 1). Ashmore Reef is situated on a platform projecting from the westernmost ridge of the Sahul Shelf, averaging about 50m depth, with drop-offs to 200m almost immediately to the west and south. The prevailing swell and wind is from the south or southeast, which is reflected in the reef's morphology, being orientated east-west, with the outer reef best defined on the southern and southeastern margins. Maximum spring tidal range is 4.7m, and there is no impounding of water within the lagoon due to several large breaks in the outer reef.

The *Lithothamnion* reef crest is unbroken on the south and southeastern sides, with some coral boulder accumulations on the windward side, whereas it is broken by several passages on the northern (leeward) side, leading into two shallow lagoons (maximum 46m deep), many submerged patch reefs ('bommies'), and three low, vegetated, permanently exposed sand cays. The southern outer reef slope is initially gentle, producing a broad shelf 150m wide with extensive spur and groove formations, before dropping down more steeply in close proximity to the reef. Abutting the inner side of the southern reef crest is a reef flat composed of coral rubble and slabs, coral sediments and live coral pools. The inner

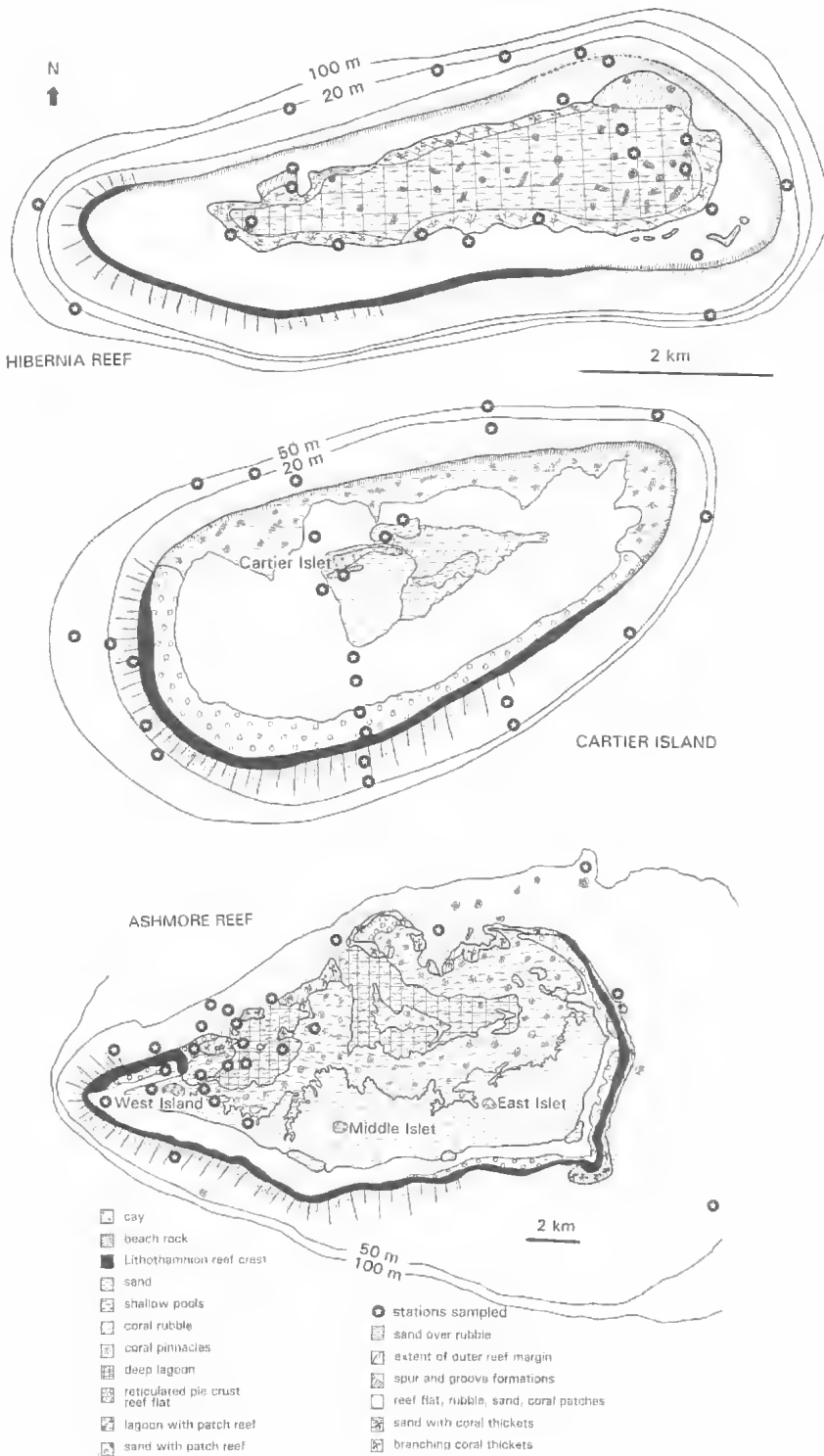


FIG. 1. Geomorphology of Hibernia, Cartier and Ashmore Reefs, Sahul Shelf, indicating major habitat types, compiled from aerial photographs (Australian Survey Office), Russell & Hanley (1992), Berry (1993), and from unpublished collection data (NT Museum, Darwin).

sand flat is very extensive, occupying possibly half the inner reef area, composed of carbonate sediments (mostly foraminiferan and mollusc debris), sparse *Thalassia* beds and algal turf. The macrobenthos here appears to be poor in structure and diversity. The northern outer reef slope is initially sheer but then the slope tapers to 50m depth, becoming continuous with the Sahul Shelf. The northern reef flat is more narrow, with little or no inner sand flat, and generally carries a richer benthos than does the sand flat on the southern margin (compiled from NT Museum unpublished data, and Berry, 1993).

**Cartier Island.** The reef is orientated east-west, lying on a platform about 50-70m deep projecting from the western edge of the Sahul Shelf, and is also exposed to swell and wind predominantly from the southern side. This windward part of the reef lies close to the edge of the continental slope, rising directly from about 180m from the south. However, Cartier Island has a very different geomorphology from both Ashmore and Hibernia Reefs (Fig. 1).

It is an oval-shaped raised platform reef, 4.5km long, 2.3km wide, lacks a lagoon, and possesses a single unvegetated sand cay that becomes submerged during spring tides. The *Lithothamnion* reef crest is only noticeably developed on the island's southwest, which also has an extensive coral boulder zone behind the reef crest. The outer reef slope on the island's south and west is substantially more extensive than that of Ashmore Reef, running about 500m seawards from the reef crest. Here there are extensive spur and groove formations and many large caverns between 10 and 30m depth. On the island's southeast, the outer reef slope is much narrower, dropping vertically to about 200m depth in a very short distance, whereas on the northern side it is almost sheer for about 30m depth but then the plateau levels at about 50-70m, prolific coral substrate merging into coralline sand. The outer reef margins on the island's north and east are diffuse, composed of consolidated pavement leading almost directly into sand and patch reef. An extensive rubble-sand-patch reef flat occupies most of the island's subtidal zone including two small shallow pools. Abundant *Thalassia* and phototrophic sponges were present on the reef flat (compiled from NT Museum unpublished data, Russell & Hanley, 1992, and Berry, 1993).

**Hibernia Reef.** It lies on the northwestern edge of the Sahul Shelf, rising from about 100m depth on all sides but dropping to 300m quite close to the northwestern edge of the reef. Hibernia Reef

is a raised platform reef, 7.7km long, 2.2km wide, with a nearly continuous outer reef around its perimeter, a deep lagoon, and no cay (Fig. 1). The *Lithothamnion* reef crest is well defined only along the southern and western margins, indicating that the prevailing swell and wind may come from this direction.

Although virtually continuous, with well developed coral boulders cemented the reef flat, the reef margin is sunken slightly on its north-eastern edge, allowing limited vessel passage into the lagoon, but there is obvious impounding of water within the lagoon during low tide. The lagoon is large, occupying more than half the reef's area, and deep (although not yet completely surveyed it averages about 30m depth, dropping to below 60m in places). Surrounding the inner margin of the reef, relatively homogenous on all sides, is a well developed reef flat. There is an extensive back reef margin of branching coral thickets at both the western and eastern margins, although in the west these thickets drop quickly to very fine coralline sand slopes, and at the northeast inner margin there is an extensive coral scree slope forming the lagoon entrance. Throughout the lagoon are large patch reef pinnacles, rising 30-50m from the lagoon floor, a dominant feature of the lagoon. The outer reef slope on the southern and western sides of Hibernia Reef is extensive, although spur and groove formations were not seen to be as well developed as the other reefs. On the northern side there is a sheer slope to about 50m, whereas on the eastern side rubble seems to dominate the outer reef area (compiled from NT Museum unpublished data, and Russell & Hanley, 1992).

#### DISTRIBUTION PATTERNS OF MARINE INVERTEBRATES

From the known distributions of a few marine invertebrate groups on the outer shelf reef systems of the western continental margin (e.g. Wilson, 1978; Berry, 1986, 1993; Wilson & Allen, 1987; Morgan & Wells, 1991; Pearce & Walker, 1991; Morgan, 1992; Marsh et al., 1993), several biogeographic models have been proposed and a number of pertinent factors have been identified that potentially contribute to these distributions.

It is worthwhile here to briefly summarise these factors, as they relate to sponge populations, since this information is relevant to the interpretation of species distribution patterns.

**Dispersal potential.** Phyla with both demersal and pelagic larval strategies are known to have

differing distributions and dispersal abilities. This explanation has been used to (partially) explain observed differences in distributions of echinoderms on some of these oceanic, outer shelf coral reefs of Western Australia (Marsh et al., 1993). By comparison, phyla with pelagic larval strategies may be much more widely distributed throughout Indo-west Pacific reef systems (e.g. corals). The third dispersal strategy, phyla with only short-lived, demersal larvae (such as sponges with a creeping blastula larva), pose an enigma in terms of resolving their potential for only short-range dispersal versus confirmed observations on relatively wide distributions for a small number of species.

Both vivipary (brooding larvae) and ovipary (broadcasting gametes) are common sexual reproductive strategies in sponges. Over short distances (or short periods of time) sexual reproductive products are undoubtedly effective in recruitment of reef sponges, but for long range dispersal their effectiveness is questionable [short lived demersal larvae, short lived gametes (e.g. about <24 hours)]. However, it is suspected that asexual (clonal) modes of dispersal are widespread, particularly in tropical sponge populations (e.g. Battershill & Bergquist, 1990), where fragments of adult sponges 'tumbleweed' across the substrate (although pelagic rafting in sponges is probably minimal; Boury-Esnault & Lopes, 1985). This does not explain how allegedly widely distributed Indo-west Pacific species are able to cross deep water barriers, and this is a question pertinent to dispersal of 'coral reef sponges' separated by deep troughs (e.g. New Caledonia and Great Barrier Reef).

*Survivorship and growth.* Although commensals on sponges are very common (including shrimps, crabs and holothurians), predators of sponges are known only to include fishes, turtles and a few other invertebrates such as nudibranch molluscs (e.g. Randall & Hartman, 1968; McClintock, 1987). Their fixed, sedentary lifestyle precludes sponges from actively evading predators or defending themselves, but they are thought to be capable of doing so using an array of noxious chemicals (e.g. Bakus, 1981; Bakus et al., 1989), which, Bakus & Ormsby (1994) hypothesise, have evolved for this specific purpose. But these 'biologically active' chemicals are also known to be important as offensive mechanisms in competition for space (e.g. Buss, 1976), and this hypothesis now has some good empirical support [such as their prevalence in crowded, cryptic communities versus exposed,

open ones (e.g. Uriz et al., 1991)]. Whichever hypothesis is correct, sponge survivorship appears to be strongly chemically mediated.

Sponges are predominantly heterotrophic, obtaining their nutrients from filter feeding suspended particles in the water column. As heterotrophs many species are efficient in surviving in high silt, high energy environments, but they are also relatively slow growing as compared with other benthic marine invertebrates such as ascidians and corals. Heterotrophic sponges do not generally compete well with scleractinian corals, for example, in clear waters (the latter have a competitive advantage in using nutrients produced by the photosynthetic activities of their symbiotic zooxanthellae).

Autotrophic (phototrophic) sponges obtain some nutrients from the photosynthetic by-products of symbiotic cyanobacteria. Unlike most heterotrophic species, autotrophs have relatively fast growth rates and are the predominant primary producers in some clear water reef habitats (e.g. reef flats) (Wilkinson, 1987). Autotrophs are more efficient competitors in these habitats, but their distribution is severely restricted to shallow, clear waters. Generally, however, sponges survive well in high energy environments and under relatively adverse conditions (surge, swell, current, sediment loads). These conditions often cause fragmentation and fragments can readily disperse and reattach to the seabed.

*Biogeographic affinities.* Precise biogeographical affinities of the northern Australian sponge fauna are still uncertain, although it is now clear that it is composed of several very different elements (Hooper & Lévi, 1994). Lévi (1979) and Wiedenmayer (1985) speculated that this fauna was predominantly southeastern Indonesian in origin, but more recent empirical evidence indicates that there are relatively higher levels of endemism than expected, ranging from 30-50% (varying between particular families (Hooper, 1991), with small regional enclaves of endemic species along the western and northwestern coasts (e.g. Houtman-Abrolhos Islands, Shark Bay, Darwin Harbour; Hooper & Lévi, 1994). By comparison, other areas appear to have very few indigenous species (e.g. Gulf of Carpentaria), and these differences are probably at least partly due to the differences in age of the Australian coastline, as described and illustrated by Jones & Torgersen (1988). This explanation is plausible to account for the colonisation and affinities of the sedentary marine invertebrates,



such as sponges, on these western oceanic coral reefs, as they were once suspected of being connected by extensive emergent reefs and shallow-water shoals to the Pleistocene continental coastline (e.g. Butlin, 1989).

It is expected that the three reefs investigated in this study would contain a mixture of both Indonesian 'colonising' species and Australian 'endemic' species, lying as they do on the northwestern margin of the Australian plate. This mix of faunas has been demonstrated in several other phyla of marine invertebrate, such as molluscs (e.g. Wells, 1986), crustacea (e.g. Morgan & Wells, 1991) and echinoderms (e.g. Marsh et al., 1993), but not previously for the sponge fauna. Furthermore, because these three coral reef systems are in close proximity to each other, each less than about 50km apart and interconnected by the shallow Sahul Shelf with its numerous submerged shoals, it is expected that each reef would contain the same, or at least very similar, sponge species.

This null hypothesis is not upheld by present data.

*Habitat availability.* Overlaying these biogeographical relationships are complex patterns related to specific ecological requirements of particular species. Coral reefs are well known for their heterogeneity (Huston, 1985), and typically contain many more potential niches than most temperate ecosystems. Sponges occupy many of these niches in coral reef systems, some opportunistic (growing in many habitats on the reef) and some highly specialised (restricted to one or few). Examples of the latter include: encrusting mats found on shallow water beach rock; seagrass beds; burrowing into mud and other soft sediments; bioeroding coralline substrates; cryptic encrusting (sciaphilic) species; 'living fossil' (reef-building) coralline species found at the base of most coral reefs; and the remarkable shallow-water autotrophic fauna. The ecology and distribution of these autotrophic species, suited to clear water coral reef habitats, has been well documented on the Great Barrier Reef (e.g. Wilkinson 1987, 1988; Wilkinson & Cheshire, 1989; Bergquist et al., 1988), but prior to the present work it was not known whether these were also prevalent on the coral reefs of the western continental margin. By comparison, the species composition of the inshore, more turbid water sponge faunas differs between the west and east coasts of Australia (e.g. Hooper, 1991; Hooper & Lévi, 1994), which may be at least partly explained by the very different geological

histories of the tropical reefs on both sides of the continent, particularly reflected by the absence of a barrier reef on the west coast (Edgerley, 1974; Burrett et al., 1991).

Both opportunistic and ecologically specialised sponge faunas have been recorded from many Indo-west Pacific coral reefs, from which earlier workers concluded that general distributions of 'coral reef sponges' were relatively homogenous across the Indo-west Pacific (e.g. Burton, 1934). This is implicit in much of the older literature, whereas it is shown in this study that the composition of the reef sponge fauna may vary considerably depending on the presence or absence of particular habitats.

#### OBSERVED DISTRIBUTION PATTERNS AND AFFINITIES OF THE SPONGE FAUNA

Prior to these present surveys the sponge fauna of Ashmore, Cartier and Hibernia Reefs was unknown. This study collected 139 species of sponges (although only 138 are differentiated, *X. testudinaria* and *X. bergquistia* combined as they could not be distinguished from video records), belonging to 77 genera and 38 families (Table 1). Each reef system contains the following number of species: Cartier Island 74 species, Hibernia Reef 73 species and Ashmore Reef 51 species. Contrary to expectations, however, the similarity between the faunas on each of these reefs was low (Fig. 2).

These discrepancies in faunal composition might be an artifact of low sample sizes, whereby accurate comparisons between reefs might not be possible due to the relatively low number of stations from which sponges were recorded. 76 stations (from a total of 113 stations sampled) contained sponges: Cartier Island 26 stations, Hibernia Reef 24 stations, and Ashmore Reef 26 stations. Whilst this explanation is plausible for comparison between Ashmore Reef and the Cartier-Hibernia collections (where only 96 samples of 51 species were collected from Ashmore Reef, no underwater video record was made, and collections were made over three separate trips), it certainly is not true for the comparison between Cartier Island and Hibernia Reef (where techniques were standardised and collecting effort was comparable). It is considered that observed differences in the sponge fauna between these reefs has a real (biological) origin.

Based on their known geographical distributions the sponge fauna was divisible into four major groups.

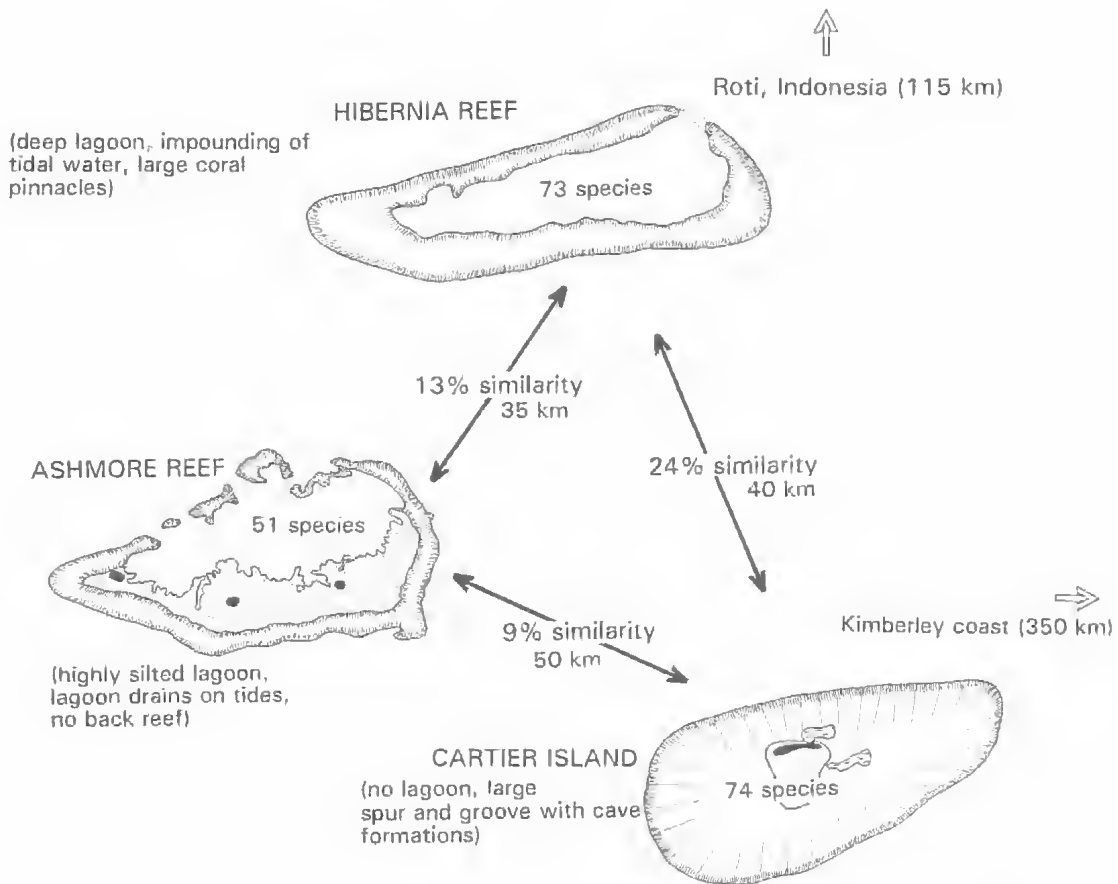


FIG. 2. Similarity in sponge faunas of 3 adjacent coral reefs, Sahul Shelf, indicating number of species on each reef and % similarity in species composition between reef systems.

1. 'Coral reef sponges'. These are widely distributed throughout the Indo-west Pacific, from Burma to New Caledonia (although some species are recorded as widespread, from Madagascar to Polynesia). The distribution of these species appears to be somehow closely linked to the actual distributions of the coral reefs themselves, although it is speculative how their supposedly short lived, poorly motile reproductive products are dispersed across this vast tract of sea (dissected by deep trenches). Most of these species are largely opportunistic, living in many or any zones on the reef. Examples of these are *Aaptos aaptos*, *Axinella carteri*, *Cinachyra australiensis*, *Cribrochalina olemda*, *Echinodictyum mesenterinum*, *Halisarca dujardini*, *Ianthella flabelliformis*, *Jaspis stellifera*, *Phakellia cavernosa*, *P. conulosa*, *Xestospongia testudinaria* and *X. nigricans*. Some 'coral reef sponges' are found associated predominantly with dead coral, on the living reef or in rubble zones, bioeroding the

calcareous substrate (e.g. *Cliona celata*, *Gelliodes fibulatus*, *Iotrochoia baculifera*, *I. coccinea*, *Microciona aceratoobtusa*, *Thalysias reinwardti*), or burrowing into both living and dead coral heads (e.g. *Aka mucosa*, *Oceanapia amboinensis*, *Myrmekioderma granulata*, *Spirastrella vagabunda*). All these groups are relatively well documented in both the contemporary and older literature.

2. *Autotrophic sponges*. As expected from literature on other coral reefs (e.g. Wilkinson & Cheshire, 1989), autotrophic species were a prevalent (visually dominant) component of the sponge fauna, with most species recorded from all three reefs. These sponges (with representatives from many families of Porifera), have symbiotic cyanobacteria within their tissues and utilise some or all of the micro-organisms' photosynthetic products for their own nutrition. Thus they are capable of relatively fast growth rates, large individual biomass, large local

population size, and they are apparently responsible for a large proportion of the coral reef's total net primary productivity (e.g. Wilkinson, 1987). Autotrophic sponges are generally restricted to the reef's shallow waters, such as shallow lagoons, inner sandy zones, and intertidal zones on the reef flat, and they include species such as *Carteriospongia foliascens*, *Dysidea herbacea*, *Haliclona cymiformis*, *Pericharax heterorhaphis*, and *Phyllospongia papyracea*.

Our present understanding of 'coral reef sponges' derives mainly from knowledge of both these groups (1 and 2), and yet together they account for only 16% of species diversity within the Ashmore, Cartier and Hibernia Reef systems.

3. *Coastal and shelf species*. 25% of the other species recorded in these surveys are known to be more-or-less widespread in tropical Australasia, found on the more turbid coastal reefs and the shallow continental shelf (e.g. a *Cliona* sp., *Didisicus aceratus*, *Higginsia scabra*, *Raphidotethya enigmatica*, *Reniochalina stalagmitis*, *Teichaxinella labyrinthica*).

4. *'Restricted sponge fauna'*. The greatest diversity (59%) of sponges in these reef systems consists of species with restricted or specialised habitats, such as in sheltered waters on the floor of deep lagoons, at the base and on the sides of pinnacles or patch reefs within deep lagoons, in spurs and grooves on the reef front, in caves on the upper reef slope, or associated with seagrass beds in shallow sand flats. Some of these habitats are not present in all reef systems (Fig. 1), and therefore these more restricted species are obviously not present either. This component of the fauna is very poorly known in the literature: species are either undocumented, with several new species from this region already confirmed, or with only a few other isolated records in the literature.

The hypothesis, that the composition of the sponge fauna is largely related to the geomorphology of each reef, is further supported by specific anecdotal examples. *Plakortis mammillaris*, for example, was only found on the outer reef slope, in spur and groove formations and in caves on the forereef, which are best represented at Cartier Island, but was not found at either Hibernia or Ashmore Reef. Conversely, *P. nigra* was collected from Hibernia and Ashmore Reefs, on fringing and patch reefs within the lagoon, but was not seen at Cartier Island which has no lagoon. Similarly, *Asteropus sarassinorum* is a dominant non-scleractinarian species of the benthos in the deeper parts of the lagoons of Hibernia

and Ashmore Reefs, but completely absent from Cartier Island. Differences in the geomorphology of these reefs (e.g. the extent of development of the fore-reef slope, presence and absence of a lagoon system) may be directly responsible for these observed differences in the sponge fauna.

Given the close proximity of the three reefs to each other, each lying at about the same distance from the edge of the continental shelf, and each interconnected by a shallow platform with a number of submerged shoals interdispersed, it is unlikely that any differences in dispersal of reproductive bodies between the reefs could account for the observed differences in sponge species composition. Conversely, it is suggested here that the relatively low levels of similarity between the sponge faunas of Ashmore, Cartier and Hibernia Reefs is related to the presence or absence of particular habitats on each reef (i.e., both major and 'minor' differences in the geomorphology of the reefs). The most obvious differences in reef geomorphology are seen between Cartier Island and the other two reefs (the former with large coral caves and overhangs in the spur and groove formations of the fore-reef zone, and an extensive reef flat; the latter with extensive, relatively deep water lagoons and their associated sheltered-water habitats); less striking, but just as 'effective', are the differences between Ashmore Reef and Hibernia Reef (the former with an unusual highly sedimented lagoon, covering most of its back reef slope - an area which usually has very rich coral growth; and the latter with a nearly continuous outer reef margin, and extensive system of patch reefs within the lagoon). Thus, the concept of a relatively homogenous, ubiquitous 'coral reef sponge fauna', implied in the literature, is an oversimplification; ecological specialisation, as a requirement for survival, is probably more important than previously recognised for sponges (cf. Lévi, 1979; Wiedenmayer, 1985).

That only 25% of all species recorded in this study are known from either (or both) tropical Australian and southern Indonesian waters supports the notion that biogeographic affinities of the sponge fauna on the northwestern continental shelf is not overwhelmingly that of southern Indonesia (Hooper & Lévi, 1994), as proposed by both Wiedenmayer (1985) and van Soest (1990), but they contain a more complex mix of Australian 'endemics', Indonesian 'invaders', widely distributed oceanic species ('coral reef sponges').



## CONCLUSIONS

Extrapolation of these findings to a conservation strategy for marine resources is appropriate in this forum. One of the main stated functions of a system of marine parks is to provide a reservoir of genetic diversity, to repopulate adjoining areas, as well as to protect particular habitats, marine processes and rare and endangered species (Ivanovici, 1984). Within the various biogeographical provinces there are often small 'representative' habitats set aside as protected areas, on the basis of being 'typical' and containing sufficient resources to fulfil their functions as genetic reservoirs. This is the existing situation for Ashmore Reef, declared a National Nature Reserve in 1983, with the primary stated purpose to protect marine and terrestrial fauna and flora, to protect against possible overfishing, and to act as a representative of an oceanic, outer shelf reef and atoll rising from the edge of the Sahul Shelf. Evidence presented here questions the validity of preserving only a single reef as being 'representative' of, and maintaining genetic resources for, a system of reefs. For one group of marine invertebrates at least, and supported to a some extent by data from other groups [echinoderms (Marsh et al., 1993); molluscs (Wells, 1993)], it is suggested that 'adequate biodiversity' may not be contained within a single reef system. Both subtle and major differences in reef geomorphology appear to substantially influence some faunas. Marine sanctuaries should be designed to contain enough diversity of reef types to provide a true reservoir of genetic diversity.

## ACKNOWLEDGEMENTS

I thank Dr Lyle Vail (now at Lizard Island Research Station), Dr Russell Hanley and Dr Barry Russell (NT Museum), Principal Investigators of various expeditions funded by the Australian National Parks and Wildlife Service (Australian Nature Conservation Agency), for providing me access to these remote faunas; Dr Paddy Berry (WA Museum), through Dr Barry Russell, for access to an unpublished manuscript on Ashmore Reef, and to some of the authors contributing to the Ashmore Reef survey, Mrs Loizette Marsh, Dr Gary Morgan and Dr Fred Wells for permitting me to cite some of their work in press; Dr C.C. Lu (Museum of Victoria) for access to the Taiwanese RV 'Hai Kung' collections; the skipper and crew of the FV 'Rachel' for

great company; and Ms Cathy Johnston, Ms Anne-Marie Mussig, Dr Lyle Vail and Dr Helen Larson for assisting in collecting and photographing sponges from these reefs.

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TABLE 1. List of sponge species collected from Cartier, Hibernia and Ashmore Reefs, showing distribution within the three reefs and extra-limital distribution where known. Species numbers refer to as yet unidentified, possibly new species in NTM and QM collections.

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SPECIES	REEF SYSTEM			
	CARTIER	HIBERNIA	ASHMORE	Extra-limital distrib.
Class Calcarea				
Order Leucettida: Family Leucettidae				
<i>Pericharax heterorhaphis</i> (Polejjaeff)	+	+	+	(N coast, GBR, S Indonesia)
Class Demospongiae				
Order Homosclerophorida: Family Plakinidae				
<i>Plakortis mammillaris</i> (Lendenfeld)	+	—	—	(GBR, E Indonesia)
<i>Plakortis nigra</i> Lévi	—	+	—	(E Indonesia, Red Sea)
'Order Lithistida': Family Theonellidae				
<i>Theonella cylindrica</i> Wilson	+	+	—	(S Philippines, Indonesia)
Order Spirophorida: Family Tetillidae				
<i>Cinachyra australiensis</i> (Carter)	+	+	—	(NE & NW coasts, E & W Indonesia, Malay., SW Pac.)
<i>Cinachyra schulzei</i> (Keller)	+	—	—	(E Indonesia)
<i>Cinachyra</i> sp. 333	—	—	+	(unknown)
<i>Cinachyra</i> sp. 409	—	—	+	(unknown)
<i>Craniella</i> sp. 402	—	—	+	(NW shelf)
<i>Raphidotethya enigmatica</i> Burton	—	—	+	(NE & NW coasts)
<i>Tethyopsilla</i> sp. 1105	+	—	—	(unknown)
<i>Tetilla</i> sp. 594	—	+	—	(NW coast)

SPECIES	REEF SYSTEM			
	CARTIER	HIBERNIA	ASHMORE	Extra-limital distrib.
Order Astrophorida: Family Coppattiidae				
<i>Asteropus sarassinorum</i> Thiele	—	+	+	(E Indonesia)
<i>Asteropus</i> sp. 1091	+	+	—	(unknown)
<i>Jaspis stellifera</i> (Carter)	+	+	—	(Indo-West Pacific)
<i>Jaspis</i> sp. 1005	—	+	—	(GBR, New Caledonia)
<i>Jaspis</i> sp. 1093	+	—	—	(unknown)
<i>Jaspis</i> sp. 1097	+	+	—	(unknown)
Order Astrophorida: Family Ancorinidae				
<i>Ancorina</i> sp. 797	—	—	+	(unknown)
<i>Stelletta globostellata</i> Carter	+	+	—	(E Indonesia)
Order Hadromerida: Family Chondrillidae				
<i>Chondrosia</i> sp. 1083	+	—	—	(unknown)
Order Hadromerida: Family Clonidae				
<i>Cliona celata</i> Grant	+	+	—	(NW coast)
<i>Cliona</i> sp. 32	—	+	—	(NW & NE coasts)
<i>Cliona</i> sp. 114	—	+	—	(NW coast)
Order Hadromerida: Family Suberitidae				
<i>Aaptos aaptos</i> (Schmidt)	+	+	—	(widespread Indo-West Pacific)
<i>Suberites</i> sp. 634	—	—	+	(unknown)

TABLE 1. (continued)

SPECIES	REEF SYSTEM			Extra-limital distrib.
	CARTIER	HIBERNIA	ASHMORE	
Order Hadromerida: Family Spirastrellidae				
<i>Spirastrella vagabunda</i> (Ridley)	+	—	—	(NW coast, E Indonesia, S Philippines, W Pacific)
<i>Spirastrella</i> sp.89	—	+	—	(NW coast)
<i>Spirastrella</i> sp. 480	—	—	+	(unknown)
Order Hadromerida: Family Tethyidae				
<i>Tethya</i> sp.939	+	—	—	(Gulf of Thailand)
Order Hadromerida: Family Latrunculiidae				
<i>Latrunculia</i> sp.1048	—	+	—	(PNG)
Order Halichondrida: Order Desmoxysiidae				
<i>Higginsia</i> sp.1059	+	—	—	(unknown)
<i>Higginsia scabra</i> Whitelegge	+	—	+	(NW coast, GBR)
<i>Myrnekioderma granulata</i> (Esper)	+	+	—	(Indo-West Pacific)
<i>Myrnekioderma</i> sp.1092	+	—	—	(unknown)
Order Halichondrida: Family Axinellidae				
<i>Acanthella</i> sp.836	+	+	—	(S Australia)
<i>Axinella</i> sp.26	—	—	+	(S Australia)
<i>Axinella carteri</i> (Dendy)	+	+	+	(Indo-Pacific)
<i>Axiaella</i> sp.1089	+	—	—	(unknown)
<i>Pseudaxinella</i> sp.662	+	—	—	(GBR)
<i>Phakellia cavernosa</i> (Dendy)	+	—	+	(NW coast, GBR, Thailand, New Caledonia, E Indonesia)
<i>Phakellia canulosa</i> Dendy	+	+	—	(Indo-Pacific)
<i>Phakellia dendyi</i> Bergquist	+	+	—	(NZ, PNG, NW coast, S Philippines)
<i>Phakellia</i> sp.646	+	—	—	(GBR, PNG, NW coast)
<i>Remiochalina stalagmitis</i> Lendenfeld	+	+	+	(N & NW coasts)
<i>Remiochalina</i> sp.172	+	—	—	(NW coast)
<i>Remiochalina</i> sp. 798	—	—	+	(unknown)
<i>Teichaxinella labyrinthica</i> (Dendy)	+	—	—	(NW shelf)
<i>Teichaxinella</i> sp. 1012	—	—	+	(unknown)
Order Halichondrida: Family Halichondriidae				
<i>Didiscus oceratus</i> (Ridley & Dendy)	+	—	—	(NW coast)
Order Agelasida: Family Agelasidae				
<i>Agelas mauritiana</i> Carter	+	—	—	(Indo-Pacific)
Order Agelasida: Family Astroscleridae				
<i>Astrosclera willeyna</i> Lister	+	+	—	(GBR, Christmas I., E Indonesia)
Order Poecilosclerida: Family Desmacellidae				
<i>Bienna</i> sp. 793	—	—	+	(NW shelf)
Order Poecilosclerida: Family Desmacididae				
<i>Batzella</i> sp.1096	+	+	—	(unknown)
<i>Desmacidon</i> sp.980	—	+	—	(GBR, NW coast)
<i>Desmaapsamma</i> sp.800	+	+	+	(NW shelf)
<i>lotrochota baculifera</i> Ridley	+	+	+	(Indo-West Pacific)
<i>lotrochota coccinea</i> (Carter)	+	+	—	(Indo-West Pacific)
Order Poecilosclerida: Family Hymedesmiidae				
<i>Hymedesmia</i> sp.1098	+	+	—	(unknown)
Order Poecilosclerida: Family Microcionidae				
<i>Microciona aceratoobtusa</i> Carter	+	+	—	(Indo-Pacific)
<i>Thalysias coppingeri</i> (Ridley)	—	—	+	(NW & NE coasts)
<i>Thalysias reinwardti</i> (Vosmaer)	+	+	—	(W Pacific—E Indonesia)
<i>Thalysias tingens</i> Hooper	—	+	—	(NW coast)
<i>Thalysias taxifera</i> (Hentschel)	+	+	—	(NW coast, E Indonesia)
<i>Antho (Dirrhopalium) ridleyi</i> (Hentschel)	—	+	—	(Arafura & Timor Seas)
Order Poecilosclerida: Family Raspailiidae				
<i>Ectyoplasia tabula</i> (Lamarck)	—	+	—	(N & NW coasts & shelf)
<i>Echmodictyum cancellatum</i> (Lamarck)	—	+	—	(NW & NE coasts, E Indonesia)
<i>Echmodictyum mesenterinum</i> (Lamarck)	—	+	+	(circum-Australia, prob. Indo-West Pacific)

TABLE I. (continued)

SPECIES	REEF SYSTEM			Extra-limital distrib.
	CARTIER	HIBERNIA	ASHMORE	
Order Poecilosclerida: Family Crellidae				
<i>Crella spiculata</i> (Hentschel)	—	+	—	(GBR, NW coast & shelf, Houtman-Abrolhos Is, New Caledonia)
Order Poecilosclerida: Family Mycalidae				
<i>Areaochalina</i> sp. 795	—	—	+	(unknown)
<i>Mycale</i> ( <i>Carmia</i> ) sp. 239	—	—	+	(NW coast)
Order Haplosclerida: Family Petrosiidae				
<i>Petrosia ashmoricæ</i> (Hooper)	—	—	+	('endemic')
<i>Petrosia</i> sp. 113	+	—	—	(NW coast, Thailand)
<i>Petrosia</i> sp. 1021	—	+	—	(S Philippines)
<i>Petrosia</i> sp. 1095	+	—	—	(unknown)
<i>Petrosia</i> sp. 1103	+	—	—	(unknown)
<i>Strongylophora strongyloia</i> (Thiele)	+	—	—	(NW shelf, E Indonesia)
<i>Xestospongia exigua</i> (Kirkpatrick)	+	+	—	(GBR, PNG, NW coast, Christmas I)
<i>Xestospongia nigricans</i> (Lindgren)	+	+	+	(E Indonesia)
<i>Xestospongia testudinaria</i> (Lamarck)	+	+	+	(Indo-West Pacific)
Order Haplosclerida: Family Chalinidae				
<i>Acervachalina confusa</i> Dendy	+	—	—	(Indian Ocean)
<i>Adocia</i> sp. 171	—	+	—	(NW coast)
<i>Adocia</i> sp. 384	—	—	+	(unknown)
<i>Haliclona</i> sp. 945	+	—	—	(Burma, SW Thailand)
<i>Haliclona</i> sp. 1022	+	+	—	(S Philippines)
<i>Reniera</i> sp. 789	—	+	+	(PNG)
<i>Reniera</i> sp. 801	—	—	+	(unknown)
<i>Reniera</i> sp. 1046	—	+	—	(PNG)
<i>Haliclona cymiformis</i> (Esper)	+	+	+	(NE & NW coasts, PNG, S Indonesia, W Pacific)
Order Haplosclerida: Family Callyspongiidae				
<i>Callyspongia schulzei</i> Kieschnick	—	+	—	(NW coast, E Indonesia)
<i>Callyspongia</i> sp. 407	—	—	+	(unknown)
<i>Callyspongia</i> sp. 755	+	—	—	(Shark Bay)
Order Haplosclerida: Family Niphatidae				
<i>Amphimedon</i> sp. 881	+	—	—	(Thailand)
<i>Cribrachalina oemda</i> de Laubenfels	—	+	—	(NW coast, E Indonesia, Palau, Truk, S Philippines)
<i>Cribrachalina</i> sp. 792	+	—	+	(PNG)
<i>Cribrachalina</i> sp. 1108	—	+	—	(unknown)
<i>Gelliodes fibulatus</i> (Carter)	+	+	—	(widespread Indo-Pacific)
<i>Gelliodes</i> sp. 555	—	—	+	(unknown)
<i>Gelliodes</i> sp. 619	+	—	—	(NW coast & shelf)
<i>Gelliodes</i> sp. 1049	—	+	—	(PNG)
<i>Aka mucosa</i> (Bergquist)	+	—	—	(Indo-West Pacific)
<i>Aka</i> sp. 1102	+	—	—	(unknown)
Order Haplosclerida: Family Oceanapiidae				
<i>Oceanapia amboinensis</i> Topsent	+	+	+	(NW coast, S Indonesia)
<i>Oceanapia</i>	—	+	—	(NW coast & shelf)
<i>Pellina</i> sp. 805	—	—	+	(unknown)
<i>Pellina</i> sp. 1101	+	—	—	(unknown)
Order Dictyoceratida: Family Spongiidae				
<i>Carteriospongia flabellifera</i> (Bowerbank)	—	+	+	(GBR, PNG, E Indonesia)
<i>Carteriospongia foliascens</i> (Pallas)	—	+	+	(widespread Indo-Pacific)
<i>Dactylospongia elegans</i> (Thiele)	+	+	—	(GBR, E Indonesia)
<i>Hyrrios</i> sp. 796	—	—	+	(unknown)
<i>Phyllospongia papyracea</i> (Esper)	+	+	+	(widespread Indo-Pacific)
<i>Spongia</i> sp. 15	—	—	+	(NW coast)
Order Dictyoceratida: Family Irciniidae				
<i>Aplysinopsis reticulata</i> (Lendenfeld)	+	+	—	(N & NW coasts)
<i>Aplysinopsis elegans</i> Lendenfeld	—	—	+	(N Australia)
<i>Fascuplysinopsis reticulata</i> (Hentschel)	+	+	—	(E Indonesia, SE Qld, GBR)



TABLE 1. (continued)

SPECIES	REEF SYSTEM			Extra-limital distrib.
	CARTIER	HIBERNIA	ASHMORE	
<i>Ircinia</i> sp. 1	—	—	+	(N Australia)
<i>Luffariella</i> sp. 804	—	—	+	(unknown)
<i>Thorecta</i> sp. 11	—	—	+	(NW coast)
Order Dictyoceratida: Family Dysideidae				
<i>Dysidea arenaria</i> Bergquist	+	—	—	(GBR, Thailand, Palau Is)
<i>Dysidea granulosa</i> Bergquist	—	+	—	(Palau Is)
<i>Dysidea herbacea</i> (Keller)	+	+	+	(Indo-Pacific)
Order Verongida: Family Druinellidae				
<i>Pseudoceratina</i> sp. 190	—	—	+	(unknown)
<i>Pseudoceratina</i> sp.364	+	+	+	(NW coast)

SPECIES	REEF SYSTEM			Extra-limital distrib.
	CARTIER	HIBERNIA	ASHMORE	
Order Verongida: Family Aplysinidae				
<i>Aplysina ianthelliformis</i> Bergquist & Tizard	+	+	—	(NW coast)
<i>Aplysina</i> sp. 125	—	—	+	(unknown)
Order Verongida: Family Ianthellidae				
<i>Ianthella flabelliformis</i> (Pallas)	—	+	—	(Indo-West Pacific)
<i>Ianthella</i> sp.993	+	—	—	(GBR)
Order Dendroceratida: Family Darwinellidae				
<i>Aplysilla</i> sp.688	—	+	—	(Indo-Pacific)
Order Dendroceratida: Family Halisarcidae				
<i>Halisarca dujardini</i> Johnston	—	+	—	(? widespread Indo-Pacific)